Development of a Management Plan for Lake Sturgeon Within the Great Lakes Basin Based on Population Genetics Structure

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Abstract

To assess the population structure of lake sturgeon throughout the Great Lakes basin, standardization of genetic markers and subsequent genetic analysis has been completed. Seven other laboratories participated in standardization, with four laboratories completing the process. Standardization is an ongoing process and the infrastructure has been established for its continued success. Thirteen microsatellite markers were used to genotype spawning adults from 19 locations. Genetic distance measures were used to create a phylogenetic tree and to conduct a factorial correspondence analysis in order to explore potential management units. F statistics and G tests were used to determine the level of differentiation between population pairs. The analysis has shown a great deal of genetic structuring of lake sturgeon throughout the Great Lakes, with most rivers genetically distinct from other spawning locations. The various clustering approaches revealed the Bad and White Rivers of the Lake Superior watershed as separate from the remaining spawning populations. The analyses also revealed substantial gene exchange between the Detroit/St. Clair system and the Lower Niagara River. Conserving the genetic integrity of the different spawning populations should be an important management consideration.

Introduction

The primary goal of this study funded by the Great Lakes Fishery Trust is an assessment of the genetic population structure of lake sturgeon (*Acipenser fulvescens*) throughout the Great Lakes basin. The observed population genetic structure can then be integrated into a basin-wide lake sturgeon management plan, which will be critical for the effective management of this species. The delineation of management units based on genetic differences will help managers more efficiently target conservation strategies and better understand potential consequences of various management options. Data on levels of gene flow between spawning locations also provide insight into lake sturgeon ecology that is often difficult to detect through traditional population data measures.

The development of seven microsatellite markers (funded by the Great Lakes Fish and Wildlife Restoration Act) set the stage for this important endeavor. Microsatellite markers are a useful tool in detecting fine-scale population differences over relatively short evolutionary timescales. These seven markers, in combination with four microsatellite markers previously used in lake sturgeon studies (McQuown et al. 2003) and two newly designed microsatellite markers, all amplified disomic loci, and were used to conduct the subsequent population genetic analysis. Standardization of all 13 microsatellite markers was a critical component of the project, allowing for the integration of data obtained in this study with genetic data collected at other laboratories, resulting in a comprehensive overview of the population structure of lake sturgeon throughout the Great Lakes basin. The standardization effort has ensured, and continues to ensure, that genetic laboratories are using the same genetic markers and designating alleles consistently. Many laboratories are using different genotyping platforms and apparent allele sizes can vary depending on electrophoretic conditions (Haberl and Tautz, 1999). Standardization maintains consistent allele scoring within and between laboratories, the absence of which would otherwise severely impede the meta-analysis necessary for understanding lake sturgeon on an ecosystem scale.

The objectives of the study were to: 1) standardize microsatellite markers among genetic laboratories conducting lake sturgeon research; 2) collect samples from adults at key spawning

locations that are not targeted by other management agencies; and 3) analyze population genetic data from these sampled populations, using the standardized suite of markers.

Methods

Standardization

The 13 microsatellite markers that targeted polymorphic disomic loci were standardized among seven other genetic laboratories, and included L. Bernatchez (Université de Laval), L. Buckley (Rochester Institute of Technology), M. Ferguson (University of Guelph), A. Kapuscinski (University of Minnesota), G. Rhodes (Purdue University), K. Scribner (Michigan State University), and L. Zane (University of Padova – Italy).

Standardization kits were sent to the laboratories containing instructions for optimized PCR conditions, one to three lake sturgeon DNA extracts for each locus and their corresponding genotypes (known samples), and three lake sturgeon DNA extracts for each locus without stated genotypes (unknown samples). The known samples represented the range of alleles observed thus far, and the number of known samples varied, depending on the number of alleles possible at that locus.

Following genotyping of samples within the standardization kit, results from the participating laboratory were compared with those obtained at our laboratory and discrepancies were resolved through personal communications. Discrepancies in the scoring of unknown samples were addressed by supplying the participating laboratory with the correct genotype, allowing the laboratory to assess whether the error occurred in scoring or amplification. A workshop was originally planned for the standardization, but it became obvious this was not feasible because lake sturgeon research was a different priority for each of the participating laboratories, preventing simultaneous completion of standardization. Instead, communicating individually with each of the labs by telephone, email, and meetings at conferences proved to be better suited to the laboratories' needs. Financial resources obtained for the workshop were redirected into working individually with each laboratory and into the development of two additional microsatellite markers (that are included in the final suite of 13 microsatellites); methods and results were reported in Welsh *et al.* (2003).

Sampling

Collection of genetic samples targeted spawning lake sturgeon in candidate rivers identified by Lowie (2000). However, because there are generally low numbers of spawning populations and the spawning periodicity of lake sturgeon is infrequent, samples collected from adult sturgeon that were present in the streams at the time of spawning were considered valuable for this project. Genetic samples were collected according to the standardized protocols identified during the December 1999 workshop (Lowie 2000). A variety of sampling techniques were employed to capture lake sturgeon according to site-specific applications and techniques identified as most appropriate by the participating researchers. Bottom set gill nets fished diagonal or perpendicular to the current and baited setlines fished consistent with techniques described by Thomas and Haas (1999) were the most common methods employed. Researchers began surveying streams in 2002 and sampling continued through 2003. A target sample size of 30 fish for each stream was established by UC-Davis for the sampling component of this project. Samples collected during the course of this investigation were forwarded to the genetics laboratory at UC-Davis for analysis.

Genetic Analysis

In addition to the samples collected in this study, lake sturgeon samples analyzed in previous studies at our laboratory at UC-Davis (McQuown et al., 2003) were reanalyzed with the newly developed microsatellite markers. These sampled spawning locations include the Des Prairies River (St. Lawrence River watershed; n=14), Mattagami River (Hudson Bay drainage; n=40), Menominee River (Lake Michigan watershed; n=21), St. Lawrence River (n=54), and Wolf River (Lake Michigan watershed; n=30). Samples obtained by the Ontario Ministry of Natural Resources (T. Mosindy) from the Lake of the Woods / Rainy River system (Hudson Bay drainage; n=27) were also included in the analysis.

Collected fin clips or rays were sent to our laboratory and DNA was extracted from the samples using the Wizard® DNA extraction kit (Promega Corporation, Madison, WI, USA). Extracted DNA was then quantitated in order to standardize the concentrations for amplification, resulting in more uniform amplication. Extracted DNA was amplified with the polymerase chain reaction (PCR) using the suite of 13 microsatellite markers, according to conditions described in Welsh *et al.* (2003). Amplified products were then visualized on an MJ Research MasseStation® and alleles scored using the Cartographer© (MJ GeneWorks, Inc.) software. Allelic designations correspond to those established in the standardization kit. In addition to size standards within each lane, controls were run on each gel to ensure that scoring is consistent with the standardized results. Reactions were repeated once with increased template for samples that did not initially amplify.

Each locus within each population was tested for conformance to genotypic frequencies expected under Hardy-Weinberg equilibrium. Deviation from expected genotypic frequencies can result from: 1) the inadvertent sampling of two separate populations instead of one single population; 2) the presence of a null allele (an allele that does not amplify, often due to a mutation in the region flanking the microsatellite repeat); 3) inbreeding; 4) selection; and/or 5) small population size.

Each locus pair within each population was also tested for non-random association of alleles (linkage disequilibrium), which can indicate the occurrence of genetic drift (random changes in allele frequencies, often observed in small populations) or recently admixed populations. Both Hardy-Weinberg conformance and linkage disequilibrium were tested using the Genetic Data Analysis (GDA) software (Lewis and Zaykin, 2001).

Two methods were used to cluster populations according to genetic similarities. First, genetic distance measures (Nei, 1978; Cavalli-Sforza and Edwards, 1967) were used to assess differences in allele frequencies between populations. These distances were then used to construct UPGMA and neighbor-joining trees, representing clusters of genetically similar populations, using Tools for Population Genetic Analysis (Miller, 1997) and PHYLIP (Felsenstein, 2004) software. Bootstrapping determined the replicability of tree topology, by recalculating trees after replicating the dataset with replacement and determining the number of replicates that support a certain node or branch. Second, a factorial correspondence analysis was also conducted (Genetix software; Belkhir et al., 2000), breaking down the genetic variation into a minimal number of components that explain a maximal amount of the variation. Projection of the individuals and population means on the axes provide an exploratory tool for identifying clusters and potential management units.

Genetic differentiation between the spawning locations was assessed using F statistics (F_{ST}) , which measure the proportion of heterozygosity that can be explained by population subdivision. Although F_{ST} can range from zero to one, subspecies status is often conferred at an

F_{ST} of 0.25. Log ratio likelihood tests (G tests) were used to test the significance of the observed genetic differences between population pairs, using the software FSTAT (Goudet 2001).

The small sample sizes obtained from the Spanish, Thessalon, and Nottawasaga Rivers within the Lake Huron basin result in an inaccurate assessment of allele frequencies in those populations. To determine to which populations these sampled individuals were most similar, assignment testing through Bayesian methods was implemented, using the GeneClass2 software (Piry et al., submitted).

Results

Standardization

Four of the seven laboratories (excluding our laboratory) have completed the standardization process. Two of the remaining laboratories have received the standardization kit, but have not yet begun the process due to lake sturgeon research currently being a low priority in their laboratory, while the other remaining laboratory has recently begun the process. Genotyping platforms used for standardization ranged from the MJ Research BaseStation, Hitachi FMBIOII, ABI 377, and ABI 3700. The four laboratories that have completed standardization did not use all 13 microsatellite loci. Reasons for loci exclusion include study completion prior to development of the new markers, difficulty obtaining consistent amplification with certain loci, or a small study scope not requiring the use of many loci. Accuracy in the scoring of unknown samples at the four laboratories resulted in the following percentages of correct scoring: 75%, 83%, 93%, and 100%.

Sampling

Sampling for lake sturgeon was conducted in a total of twenty-five (25) streams in the Lakes Superior, Huron, Erie and Ontario basins during spawning seasons in 2002 and 2003. Of this total, thirteen streams were sampled within the Lake Superior watershed, seven within the Lake Huron watershed, two within the Lake Erie watershed and three from the Lake Ontario watershed during the two years of sampling. The target of 30 tissue samples was achieved for five Lake Superior streams (Bad R., White R., Kaministiquia R., Black Sturgeon R., and Pic R.), one Lake Huron stream (Mississaugi R.) and two from the Lake Erie watershed (St. Clair R. and Detroit R.). The remainder of the streams where lake sturgeon samples were collected produced less than the target sample size but many produced adequate samples for comparative analysis and is discussed in the genetic analysis and discussion sections of this report. Table 1 provides a complete summary of the streams sampled and the number of samples collected in each during the 2002 and 2003 spawning seasons.

Agencies participating in sampling efforts during the 2002-03 field seasons included: US Fish and Wildlife Service, Fisheries and Oceans Canada, Ontario Ministry of Natural Resources, Pukaskwa National Park, Pic River First Nation, Bad River Band of Lake Superior Chippewa, Grand Portage Band of Lake Superior Chippewa, the Great Lakes Indian Fish and Wildlife Commission, US Coast Guard, US Geological Survey Great Lakes Science Center, Ohio State University and Purdy Fisheries and the University of California-Davis.

Genetic Analysis

The number of alleles observed ranged widely between loci and between populations. The loci AfuG 195 and Aox 27 had the smallest number of alleles (3), while several loci (AfuG 9, Afu 68, and AfuG 122) had 11 or 12 (Afu68b) alleles. The rivers in the Hudson Bay drainage

(Mattagami and Lake of the Woods/Rainy River) had the lowest genetic diversity, in terms of average number of alleles observed (3.61 and 3.85, respectively), while the St. Lawrence River had the greatest diversity, with an average number of alleles of 5.38. Table 2 contains allele frequencies for each locus in each population. Heterozygosity is also a measure of genetic diversity, and average expected heterozygosity over all loci in each population ranged from 0.49 (Lake of the Woods/Rainy River) to 0.63 (Lower Niagara).

One locus (AfuG 122) was significantly out of Hardy-Weinberg equilibrium in most populations (Table 3), due to an excess of homozygotes. This is most likely attributable to the presence of a null allele. In addition, Afu 68 is also significantly out of Hardy-Weinberg equilibrium in six populations; inheritance testing had revealed the presence of a null allele at this locus (Pyatskowit et al. 2001). In the St. Lawrence River population, three loci are in disequilibrium, with one locus having an excess of heterozygotes. The combination of heterozygosity excesses and deficits in one population indicates that the location may consist of more than one spawning population, each having substantial allele frequency differentials. The remaining deviations from Hardy-Weinberg equilibrium were at isolated loci in a few populations. Inbreeding would be an unlikely explanation because all loci should be impacted; instead, these loci could be linked to a locus (or loci) under selective pressure or a null allele could be present in those populations. Three locus combinations in the Bad River population and two locus combinations in the Kaministiquia River were in linkage disequibrium (p<0.006; significance threshold determined after sequential Bonferonni correction), with non-random association of alleles at different loci. The observed linkage disequilibrium could indicate a recently admixed population or could be due to a historic genetic bottleneck.

Between-population comparisons indicated that most spawning populations were genetically distinct from other populations (Table 4). Due to insufficient power from small sample sizes, the Spanish, Nottawasaga, and Des Prairies Rivers could not be distinguished from many populations, and the Batchawana and Goulais Rivers could not be distinguished from each other. Other populations that are genetically indistinguishable include the: 1) Bad and White Rivers; and 2) Detroit, St. Clair, and Lower Niagara Rivers.

The UPGMA and neighbor-joining trees display genetic relationships between the different populations (Figures 1 and 2). A well-supported split between the Hudson Bay drainage and the Great Lakes basin is observed. Moderately-supported splits are observed within the Lake Superior basin, indicating genetic structuring within the lake basin, and the majority of the Lake Superior spawning locations group apart from the remainder of the Great Lakes. The Bad and White Rivers consistently group together, and their genetic uniqueness is best demonstrated through their separation from the rest of the Great Lakes depicted through factorial correspondence analysis (Figure 3). The remainder of the Great Lakes basin has low-support groupings, which can indicate high genetic variation between the different populations, making it difficult to identify populations that are most similar.

Success in the assignment of the Lake Huron rivers with small sample size (Spanish, Nottawasaga, and Thessalon Rivers) to their most similar spawning population varied. Six of the eight Nottawasaga River samples were unable to be strongly assigned to any of the populations; two of the samples, however, appeared to be most similar to samples from the Detroit/St. Clair system (96% likelihood for each of the samples). The five Spanish River samples could not be strongly assigned, indicating the Spanish River may be genetically unique from other spawning locations. The three Thessalon River samples appeared most similar to either the Batchawana or Goulais Rivers in Lake Superior (98%, 97%, and 99% likelihood, respectively).

Discussion

The standardization of microsatellite markers will help accomplish the goal of understanding lake sturgeon population structure throughout its range, by permitting the synthesis of data from multiple laboratories. Through implementation of the described methods, creation of the standardization kits is simple and the participating laboratories found the kits easy to use. If a large number of laboratories were participating simultaneously, it may have been worthwhile to develop ladders that could be mass-produced. For the relatively small number of participants in standardization, the selected method proved to be efficient. Standardization is an on-going process as standardization results will continue to be attained at laboratories where lake sturgeon research is currently a low priority, and as more laboratories undertake lake sturgeon genetics research. Through funding from the Great Lakes Fishery Trust, the infrastructure for standardization has been established, allowing for continued success into the future.

Use of the standardized markers proved informative in understanding lake sturgeon population structure on both a large and small scale. All of the populations have maintained relatively high levels of heterozygosity, perhaps due to their polyploid origins (Blacklidge and Bidwell, 1993). Most lake sturgeon spawning populations are genetically distinct, indicating that lake sturgeon may demonstrate spawning site fidelity. However, the timing and mechanisms of imprinting remain uncertain. Those populations that cannot be genetically distinguished from each other include the Bad and White Rivers of Lake Superior, and the Detroit, St. Clair, and Lower Niagara Rivers.

The Bad and White Rivers are extremely unique, and are very distinct from the rest of the Great Lakes populations, including those populations in Lake Superior. It is critical that the genetic integrity of this population be maintained, as it may represent important adaptations that could be eliminated through careless management actions. The strong similarities between the Detroit/St. Clair system and the Lower Niagara River raise the potential for the existence of a metapopulation. The lack of strong spawning site fidelity among these populations generates important questions concerning the reason for straying and/or recolonization of spawning locations.

The genetic data have revealed the importance of scale when developing management strategies for lake sturgeon. It cannot be assumed that all lake sturgeon populations within a lake basin are similar, as revealed by the significant population structure within Lake Superior. This assumption would disregard the genetic importance of the Bad and White River sturgeon. Lake Superior was the most thoroughly represented lake basin in our sample collection, and significant within-lake population structure may be revealed in other lake basins following more thorough sampling. Additionally, coordination between the different lake basins is critical because of possible genetic exchange on a larger scale, as observed between the Detroit/St. Clair and Lower Niagara populations. An ecosystem-wide approach is critical for lake sturgeon conservation. To facilitate this approach, future research should involve sampling of additional spawning populations, as well as a focus on understanding when and how spawning site fidelity occurs, prior to the implementation of irreversible management actions.

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Table 1. Lake sturgeon spawning streams sampled in lakes Superior, Huron, Erie and Ontario, and sample size from each, during the 2002-2003 spawning seasons.

Lake	Stream	Sample Size
Lake Superior		
	Bad River (Wisconsin)	148
	White River (Wisconsin)	45
	Pigeon River (Minnesota/Ontario)	2
	Kaministiquia River (Ontario)	87
	Black Sturgeon River (Ontario)	58
	Pic River (Ontario)	33
	Black River (Ontario)	1
	Little Black River (Ontario)	0
	White River (Ontario)	0
	Michipicoten River (Ontario)	1
	Batchawana River (Ontario)	7
	Chippewa River (Ontario)	1
	Goulais River (Ontario)	16
Lake Huron		
	Mississaugi River (Ontario)	96
	Nottawasaga River (Ontario)	8
	Spanish River (Ontario)	5
	Thessalon River (Ontario)	3
	Magnetawan River (Ontario)	0
	Serpent River (Ontario)	0
	Rifle River (Michigan)	0
Lake Erie		
	St. Clair River (Michigan/Ontario)	56
	Detroit River (Michigan/Ontario)	36
Lake Ontario		
	Niagara River (New York/Ontario)	21
	Black River (New York)	0
	Trent River (New York)	0

Table 2. Allele frequencies for each of the 13 microsatellite loci at each of the 19 spawning locations. Allele sizes are in basepairs. Number of samples at that locus and the number of alleles observed are listed for each population. The last column indicates the presence of a private allele, which is observed in only one of the populations. Average number of alleles for each population is listed at the end of the table.

	Allele	Matta-				Kamini-	Batcha-		Black		Menom-		Missis-	Notta-			St.		Des	St.	
Locus	(size bp)	gami	Rainy	Bad	White	stiquia	wana	Goulais	Stur	Pic	inee	Wolf	saugi	wasaga	Spanish	Detroit	Clair	Niagara	Prairies	Law	Private
AfuG 9																					
Sample Size		40	26	136	41	83	6	23	57	33	20	29	50	8	5	33	50	20	13	48	
# Alleles		5	6	4	4	6	5	6	5	6	5	9	6	4	5	6	8	6	8	8	
	124	0.06	0.08	0.27	0.33	0.06	0.42	0.04	0.04	0.05	0.05	0.07	0.09	0.06	0.20	0.14	0.20	0.13	0.08	0.19	
	128	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.02	0.00	0.10	0.00	0.01	0.00	0.00	0.00	
	132	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.03	0.03	0.00	0.00	0.10	0.00	0.01	0.00	0.04	0.11	
	136	0.00	0.00	0.00	0.00	0.04	0.17	0.11	0.00	0.02	0.00	0.03	0.00	0.00	0.00	0.03	0.05	0.03	0.08	0.08	
	140	0.14	0.00	0.50	0.54	0.25	0.17	0.59	0.40	0.33	0.43	0.03	0.48	0.44	0.30	0.39	0.33	0.38	0.27	0.06	
	144	0.60	0.21	0.10	0.07	0.36	0.17	0.13	0.13	0.21	0.38	0.03	0.24	0.38	0.30	0.38	0.27	0.15	0.19	0.26	
	148	0.03	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.05	0.13	0.03	0.02	0.00	0.00	0.05	0.05	0.03	0.12	0.09	
	152	0.18	0.37	0.13	0.06	0.26	0.08	0.11	0.41	0.35	0.00	0.03	0.15	0.13	0.00	0.02	0.08	0.30	0.15	0.17	
	156	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.03	
	160	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
	168	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	Rainy
AfuG 74																					
Sample Size		40	27	133	43	84	6	22	56	33	18	30	49	8	5	33	50	20	12	51	
# Alleles		3	3	3	3	3	2	3	3	3	3	3	3	3	3	3	3	3	4	4	
	218	0.11	0.07	0.60	0.63	0.62	0.75	0.70	0.55	0.70	0.83	0.78	0.57	0.81	0.60	0.53	0.58	0.48	0.67	0.65	
	222	0.30	0.46	0.31	0.26	0.16	0.25	0.16	0.34	0.09	0.11	0.03	0.09	0.06	0.10	0.06	0.10	0.20	0.04	0.07	
	226	0.59	0.46	0.09	0.12	0.22	0.00	0.14	0.11	0.21	0.06	0.18	0.34	0.13	0.30	0.41	0.32	0.33	0.25	0.25	
	230	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.04	
AfuG 56																					
Sample Size		40	27	136	43	82	6	22	55	33	17	30	51	7	5	33	46	20	14	50	
# Alleles		3	4	3	3	3	3	3	3	3	2	3	3	2	1	3	3	3	2	3	
	258	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	Rainy

	Allele	Matta-				Kamini-	Batcha-		Black		Menom-		Missis-	Notta-			St.		Des	St.	
Locus	(size bp)	gami	Rainy	Bad	White	stiquia	wana	Goulais	Stur	Pic	inee	Wolf	saugi	wasaga	Spanish	Detroit	Clair	Niagara	Prairies	Law	Private
	262	0.09	0.06	0.11	0.09	0.37	0.08	0.07	0.25	0.27	0.09	0.07	0.09	0.14	0.00	0.15	0.21	0.15	0.04	0.04	
	266	0.61	0.50	0.64	0.71	0.35	0.83	0.86	0.52	0.68	0.91	0.90	0.89	0.86	1.00	0.79	0.73	0.78	0.96	0.95	
	274	0.30	0.43	0.26	0.20	0.28	0.08	0.07	0.24	0.05	0.00	0.03	0.02	0.00	0.00	0.06	0.07	80.0	0.00	0.01	
Afu 68																					
Sample Size		39	27	135	42	85	6	23	57	32	21	30	49	8	5	33	50	20	14	49	
# Alleles		4	3	8	9	6	4	6	6	5	4	6	5	4	5	4	7	5	6	7	
	108	0.28	0.00	0.07	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
	112	0.47	0.91	0.53	0.50	0.44	0.00	0.22	0.42	0.47	0.62	0.40	0.24	0.44	0.10	0.39	0.42	0.43	0.54	0.55	
	116	0.00	0.00	0.00	0.00	0.00	0.42	0.17	0.00	0.00	0.02	0.02	0.03	0.00	0.10	0.00	0.00	0.00	0.00	0.04	
	120	0.00	0.00	0.01	0.04	0.01	0.00	0.07	0.28	0.22	0.05	0.12	0.20	0.25	0.30	0.06	0.13	0.10	0.18	0.14	
	124	0.00	0.00	0.07	0.11	0.15	0.33	0.28	0.08	0.11	0.00	0.13	0.28	0.25	0.30	0.39	0.29	0.15	0.11	0.07	
	128	0.08	0.02	0.03	0.01	0.35	0.17	0.00	0.06	0.02	0.31	0.32	0.24	0.06	0.20	0.15	0.08	0.23	0.11	0.14	
	132	0.17	0.07	0.04	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.10	0.04	0.04	
	136	0.00	0.00	0.19	0.11	0.01	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	
	140	0.00	0.00	0.05	0.11	0.04	0.08	0.17	0.15	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.04	0.00	
	144	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	
	152	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	White
AfuG 195																					
Sample Size		40	27	136	43	85	6	23	57	33	20	30	52	8	4	33	50	20	14	54	
# Alleles		2	2	3	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
	161	0.33	0.61	0.61	0.64	0.58	0.50	0.48	0.71	0.67	0.80	0.60	0.57	0.69	0.50	0.67	0.74	0.65	0.46	0.63	
	165	0.68	0.39	0.38	0.36	0.42	0.50	0.52	0.29	0.33	0.20	0.40	0.43	0.31	0.50	0.33	0.26	0.35	0.54	0.37	
	173	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	Bad
Afu 68b																					
Sample Size		40	27	132	41	85	6	23	57	32	20	30	50	8	5	32	49	20	13	47	
# Alleles		6	7	8	7	10	6	9	8	10	10	7	9	5	5	6	10	8	7	10	
	153	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.03	0.00	0.00	

	Allele	Matta-				Kamini-	Batcha-		Black		Menom-		Missis-	Notta-			St.		Des	St.	
Locus	(size bp)	gami	Rainy	Bad	White	stiquia	wana	Goulais	Stur	Pic	inee	Wolf	saugi	wasaga	Spanish	Detroit	Clair	Niagara	Prairies	Law	Private
	157	0.01	0.00	80.0	0.04	0.01	0.08	0.07	0.19	0.05	0.05	0.00	0.10	0.00	0.00	0.00	0.02	0.00	0.00	0.00	
	161	0.00	0.00	0.01	0.00	0.00	0.17	0.02	0.00	0.03	0.20	0.00	0.02	0.00	0.00	0.00	0.01	0.00	0.04	0.04	
	165	0.06	0.30	0.00	0.00	0.01	0.00	0.07	0.00	0.03	0.03	0.08	0.11	0.00	0.10	0.03	0.00	0.03	0.23	0.09	
	169	0.00	0.04	0.03	0.05	0.03	0.00	0.07	0.04	0.05	0.05	0.00	0.07	0.31	0.00	0.22	0.17	0.15	0.00	0.06	
	173	0.06	0.02	0.22	0.26	0.45	0.17	0.33	0.10	0.28	0.28	0.13	0.14	0.19	0.30	0.28	0.28	0.40	0.19	0.20	
	177	0.06	0.00	0.10	0.02	0.05	0.17	0.22	0.20	0.11	0.13	0.42	0.25	0.25	0.10	0.33	0.30	0.28	0.12	0.40	
	181	0.48	0.39	0.02	0.06	0.22	0.00	0.13	0.37	0.33	0.10	0.08	0.09	0.00	0.20	0.00	0.01	0.03	0.23	0.06	
	185	0.00	0.02	0.36	0.28	0.01	0.17	0.04	0.00	0.03	0.08	0.00	0.16	0.19	0.30	0.13	0.14	80.0	0.12	0.07	
	189	0.33	0.20	0.00	0.00	0.04	0.00	0.00	0.01	0.05	0.03	0.22	0.00	0.06	0.00	0.02	0.03	0.00	0.00	0.04	
	193	0.00	0.04	0.17	0.29	0.18	0.25	0.07	0.02	0.05	0.08	0.05	0.06	0.00	0.00	0.00	0.01	0.03	0.08	0.01	
	197	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	
Aox 27																					
Sample Size		40	27	135	43	71	6	22	57	33	21	30	51	8	5	33	50	20	14	52	
# Alleles		1	1	3	3	3	1	3	2	3	2	2	3	2	3	3	3	3	3	3	
	130	1.00	1.00	0.75	0.62	0.92	1.00	0.73	0.99	0.88	0.98	0.95	0.90	0.81	0.70	0.71	0.71	0.65	0.75	0.76	
	134	0.00	0.00	0.16	0.21	0.04	0.00	0.07	0.01	0.11	0.02	0.00	0.05	0.19	0.10	0.05	0.11	0.03	0.11	0.12	
	138	0.00	0.00	0.09	0.17	0.04	0.00	0.20	0.00	0.02	0.00	0.05	0.05	0.00	0.20	0.24	0.18	0.33	0.14	0.13	
AfuG 160																					
Sample Size		39	27	136	43	85	6	23	57	33	21	30	52	8	5	33	50	20	14	53	
# Alleles		3	3	4	3	4	3	3	4	4	5	4	5	3	2	2	3	2	4	4	
	127	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	Menominee
	131	0.00	0.00	0.00	0.00	0.06	0.08	0.02	0.08	0.03	0.14	0.08	0.05	0.00	0.00	0.00	0.03	0.00	0.18	0.16	World Time of
	135	0.49	0.67	0.19	0.12	0.58	0.83	0.54	0.61	0.76	0.76	0.67	0.75	0.75	0.70	0.79	0.77	0.68	0.57	0.68	
	139	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	Mississaugi
	143	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.02	0.00	0.13	0.00	0.00	0.00	0.00	0.04	0.05	
	147	0.44	0.17	0.65	0.74	0.34	0.08	0.43	0.13	0.14	0.02	0.23	0.17	0.13	0.30	0.21	0.20	0.33	0.21	0.11	
	151	0.08	0.17	0.15	0.14	0.02	0.00	0.00	0.18	0.08	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
																				00	

AfuG 112

	Allele	Matta-				Kamini-	Batcha-	-	Black		Menom-		Missis-	Notta-			St.		Des	St.	
Locus	(size bp)	gami	Rainy	Bad	White	stiquia	wana	Goulais	Stur	Pic	inee	Wolf	saugi	wasaga	Spanish	Detroit	Clair	Niagara	Prairies	Law	Private
Sample Size		38	27	128	43	83	6	18	56	33	16	28	45	8	5	30	39	19	10	39	
# Alleles		4	5	6	5	6	4	4	6	5	6	6	5	4	3	7	5	5	6	7	
	240	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	Wolf
	244	0.05	0.04	0.27	0.29	0.22	0.33	0.25	0.32	0.39	0.34	0.23	0.33	0.50	0.40	0.33	0.35	0.18	0.30	0.44	
	248	0.17	0.15	0.01	0.00	0.02	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.06	
	252	0.00	0.02	0.08	0.07	0.01	0.08	0.19	0.13	0.17	0.19	0.20	0.12	0.00	0.10	0.15	0.12	0.18	0.05	0.08	
	256	0.57	0.59	0.21	0.26	0.57	0.42	0.47	0.13	0.18	0.22	0.27	0.32	0.06	0.50	0.25	0.23	0.32	0.35	0.28	
	260	0.21	0.20	0.41	0.35	0.14	0.17	0.08	0.38	0.24	0.06	0.14	0.04	0.13	0.00	0.10	0.08	0.08	0.10	0.08	
	264	0.00	0.00	0.02	0.03	0.00	0.00	0.00	0.04	0.02	0.13	0.14	0.18	0.31	0.00	0.12	0.23	0.24	0.10	0.03	
	268	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.10	0.04	
AfuG 63																					
Sample Size		40	27	132	43	85	6	23	57	33	19	30	52	8	4	33	49	20	14	53	
# Alleles		3	3	4	4	3	4	4	4	5	4	4	4	3	3	5	5	5	4	5	
	127	0.00	0.00	0.23	0.13	0.66	0.25	0.48	0.20	0.35	0.21	0.27	0.38	0.44	0.63	0.42	0.34	0.38	0.25	0.33	
	135	0.31	0.19	0.00	0.00	0.00	0.08	0.04	0.12	0.03	0.08	0.05	0.05	0.00	0.00	0.03	0.07	0.03	0.00	0.08	
	139	0.35	0.65	0.30	0.38	0.22	0.50	0.37	0.55	0.48	0.39	0.53	0.45	0.38	0.25	0.35	0.39	0.30	0.36	0.39	
	143	0.34	0.17	0.47	0.47	0.11	0.17	0.11	0.12	0.11	0.32	0.15	0.13	0.19	0.13	0.17	0.18	0.25	0.36	0.15	
	147	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.03	0.02	0.05	0.04	0.06	
AfuG 204																					
Sample Size		40	27	130	43	85	6	23	57	33	20	30	52	8	5	33	50	20	14	53	
# Alleles		1	1	2	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
	444	4.00	4.00	0.00	4.00	0.00	0.00	0.07	0.70	0.05	0.00	0.50	0.04	0.75	0.40		0.70	0.55	0.04	0.54	
	141	1.00	1.00	0.99	1.00	0.98	0.83	0.67	0.78	0.95	0.63	0.58	0.61	0.75	0.40	0.77	0.70	0.55	0.64	0.51	
	145	0.00	0.00	0.01	0.00	0.02	0.17	0.33	0.22	0.05	0.38	0.42	0.39	0.25	0.60	0.23	0.30	0.45	0.36	0.49	
AfuG 122																					
Sample Size		38	27	118	40	82	6	20	57	32	21	30	45	7	2	29	44	20	13	49	
# Alleles		5	5	6	5	7	5	4	5	5	5	6	5	4	1	6	6	4	5	9	

	Allele	Matta-				Kamini-	Batcha-	-	Black		Menom-		Missis-	Notta-			St.		Des	St.	
Locus	(size bp)	gami	Rainy	Bad	White	stiquia	wana	Goulais	Stur	Pic	inee	Wolf	saugi	wasaga	Spanish	Detroit	Clair	Niagara	Prairies	Law	Private
	147	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.01	
	151	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	StLawrence
	155	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	Kaministiquia
	159	0.04	0.19	0.31	0.40	0.14	0.08	0.05	0.01	0.06	0.00	0.10	0.19	0.07	0.00	0.09	0.01	0.15	0.12	0.06	
	163	0.01	0.04	0.03	0.00	0.11	0.08	0.00	0.02	0.16	0.00	0.03	0.02	0.00	0.00	0.03	0.01	0.00	0.00	0.05	
	167	0.43	0.33	0.50	0.36	0.45	0.08	0.33	0.11	0.13	0.21	0.53	0.19	0.43	0.00	0.31	0.22	0.35	0.35	0.29	
	171	0.43	0.15	0.09	80.0	0.09	0.50	0.43	0.57	0.41	0.57	0.22	0.34	0.36	1.00	0.40	0.56	0.38	0.38	0.30	
	175	0.08	0.30	0.02	0.05	0.19	0.25	0.20	0.29	0.25	0.17	0.02	0.26	0.14	0.00	0.16	0.18	0.13	0.12	0.13	
	179	0.00	0.00	0.06	0.11	0.01	0.00	0.00	0.00	0.00	0.02	0.10	0.00	0.00	0.00	0.02	0.02	0.00	0.00	0.10	
	183	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	StLawrence
	187	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	Menominee
Spl 120														_	_						
Sample Size		40	27	130	35	82	6	19	55	31	18	30	49	7	5	22	36	19	14	36	
# Alleles		7	7	6	5	6	2	6	5	6	6	6	7	5	3	5	6	6	6	6	
	254	0.21	0.28	0.31	0.40	0.55	0.50	0.53	0.38	0.58	0.47	0.52	0.59	0.36	0.60	0.55	0.56	0.37	0.50	0.43	
	258	0.21	0.20	0.29	0.40	0.08	0.50	0.33	0.26	0.30	0.47	0.05	0.08	0.21	0.30	0.33	0.21	0.18	0.14	0.43	
	262	0.13	0.07	0.18	0.07	0.00	0.00	0.16	0.23	0.16	0.14	0.12	0.14	0.07	0.00	0.02	0.01	0.03	0.14	0.15	
	266	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
	274	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.15	0.01	0.00	0.00	0.00	0.00	0.00	0.04	0.22	
	278	0.23	0.04	0.04	0.01	0.04	0.00	0.03	0.00	0.02	0.03	0.07	0.08	0.21	0.00	0.14	0.04	0.18	0.11	0.10	
	282	0.39	0.09	0.18	0.14	0.15	0.00	0.00	0.09	0.00	0.03	0.10	0.02	0.00	0.00	0.00	0.03	0.11	0.04	0.03	
	286	0.01	0.46	0.01	0.00	0.03	0.00	0.03	0.04	0.10	0.00	0.00	0.07	0.14	0.10	0.11	0.15	0.13	0.00	0.00	
	290	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	Rainy
																					•
Average # alleles		3.62	3.85	4.62	4.15	4.69	3.31	4.23	4.23	4.54	4.31	4.62	4.54	3.31	2.92	4.15	4.85	4.15	4.54	5.38	

Table 3. Observed (*o*) and expected (*e*) heterozygosities for each locus at each population. Observed heterozygosities in bold and shaded yellow are significantly different from the heterozygosity expected under Hardy-Weinberg equilibrium (p<0.004, after sequential Bonferroni correction).

		Matta-				Kamini-	Batcha-		Black		Menom-		Missis-	Notta-			St.		Des	St.
Locus		gami	Rainy	Bad	White	stiquia	wana	Goulais	Stur	Pic	inee	Wolf	saugi	wasaga	Spanish	Detroit	Clair	Niagara	Prairies	Law
AfuG 9	0	0.68	0.69	0.63	0.61	0.86	0.83	0.74	0.68	0.73	0.75	0.59	0.68	0.88	1.00	0.76	0.82	0.70	0.85	0.73
	е	(0.59)	(0.75)	(0.65)	(0.60)	(0.74)	(0.80)	(0.63)	(0.65)	(0.73)	(0.68)	(0.71)	(0.69)	(0.69)	(0.84)	(0.69)	(0.77)	(0.75)	(0.87)	(0.84)
AfuG 74	0	0.43	0.63	0.57	0.60	0.64	0.50	0.59	0.68	0.45	0.33	0.40	0.57	0.38	0.80	0.48	0.66	0.65	0.42	0.53
	е	(0.56)	(0.58)	(0.54)	(0.53)	(0.55)	(0.41)	(0.47)	(0.57)	(0.47)	(0.30)	(0.36)	(0.56)	(0.34)	(0.60)	(0.56)	(0.56)	(0.64)	(0.51)	(0.52)
AfuG 56	0	0.43	0.63	0.56	0.47	0.63	0.33	0.27	0.49	0.45	0.18	0.20	0.22	0.29	0.00	0.27	0.39	0.40	0.07	0.10
	е	(0.53)	(0.58)	(0.52)	(0.45)	(0.67)	(0.32)	(0.25)	(0.62)	(0.47)	(0.17)	(0.19)	(0.20)	(0.26)	(0.00)	(0.36)	(0.43)	(0.38)	(0.07)	(0.10)
Afu 68	0	0.38	0.19	0.44	0.48	0.61	1.00	0.78	0.65	0.44	0.48	0.67	0.63	0.38	0.80	0.36	0.50	0.60	0.43	0.59
	е	(0.67)	(0.17)	(0.67)	(0.71)	(0.66)	(0.74)	(0.82)	(0.72)	(0.70)	(0.53)	(0.72)	(0.77)	(0.73)	(0.84)	(0.67)	(0.72)	(0.74)	(0.68)	(0.65)
45-0 405		0.45	0.70	0.40	0.40	0.44	0.00	0.50	0.07	0.40	0.00	0.47	0.40	0.00	4.00	0.00	0.00	0.50	0.00	0.07
AfuG 195	0	0.45	0.70	0.40	0.40	0.41	0.33	0.52	0.37	0.42	0.30	0.47	0.40	0.63	1.00	0.36	0.36	0.50	0.36	0.37
	е	(0.44)	(0.48)	(0.49)	(0.47)	(0.49)	(0.55)	(0.51)	(0.41)	(0.45)	(0.33)	(0.49)	(0.50)	(0.46)	(0.57)	(0.45)	(0.39)	(0.47)	(0.52)	(0.47)
Afu 68b	0	0.63	0.78	0.83	0.66	0.76	0.67	0.87	0.81	0.72	0.80	0.73	0.76	1.00	1.00	0.72	0.76	0.60	0.85	0.72
Ald OOD	е	(0.67)	(0.73)	(0.78)	(0.77)	(0.71)	(0.89)	(0.83)	(0.78)	(0.80)	(0.86)	(0.76)	(0.86)	(0.82)	(0.84)	(0.76)	(0.79)	(0.75)	(0.86)	(0.78)
	Ü	(0.07)	(0.70)	(0.70)	(0.77)	(0.7 1)	(0.00)	(0.00)	(0.70)	(0.00)	(0.00)	(0.70)	(0.00)	(0.02)	(0.04)	(0.70)	(0.70)	(0.70)	(0.00)	(0.70)
Aox 27	0	0.00	0.00	0.39	0.51	0.10	0.00	0.50	0.02	0.21	0.05	0.10	0.16	0.38	0.60	0.39	0.48	0.60	0.43	0.40
	е	(0.00)	(0.00)	(0.40)	(0.55)	(0.16)	(0.00)	(0.43)	(0.02)	(0.22)	(0.05)	(0.10)	(0.18)	(0.33)	(0.51)	(0.44)	(0.46)	(0.48)	(0.42)	(0.40)
		, ,	, ,	` ,	` ,	, ,	` ,	, ,	, ,	` ,	, ,	` ,	` ,	` ,	` ,	` ,	` ,	, ,	` ,	` ,
AfuG 160	0	0.79	0.48	0.49	0.42	0.47	0.33	0.30	0.61	0.36	0.24	0.43	0.38	0.25	0.60	0.30	0.36	0.65	0.50	0.28
	е	(0.57)	(0.51)	(0.52)	(0.42)	(0.55)	(0.32)	(0.53)	(0.57)	(0.41)	(0.41)	(0.50)	(0.41)	(0.43)	(0.47)	(0.34)	(0.37)	(0.45)	(0.62)	(0.50)
AfuG 112	0	0.74	0.52	0.76	0.70	0.66	0.83	0.72	0.66	0.70	0.81	0.89	0.80	0.50	0.80	0.80	0.77	0.79	0.80	0.72
	е	(0.61)	(0.59)	(0.71)	(0.73)	(0.61)	(0.74)	(0.69)	(0.73)	(0.74)	(0.80)	(0.81)	(0.74)	(0.68)	(0.64)	(0.79)	(0.76)	(0.79)	(0.79)	(0.72)
AfuG 63	0	0.73	0.52	0.67	0.63	0.52	0.67	0.70	0.70	0.73	0.74	0.33	0.67	1.00	0.75	0.76	0.71	0.90	0.79	0.68
	е	(0.67)	(0.53)	(0.64)	(0.63)	(0.50)	(0.71)	(0.63)	(0.63)	(0.64)	(0.71)	(0.63)	(0.64)	(0.68)	(0.61)	(0.68)	(0.70)	(0.72)	(0.71)	(0.72)
AfuG 204	0	0.00	0.00	0.02	0.00	0.02	0.33	0.57	0.33	0.09	0.75	0.63	0.40	0.50	0.40	0.27	0.40	0.40	0.71	0.91

		Matta-				Kamini-	Batcha-	•	Black		Menom-		Missis-	Notta-			St.		Des	St.
Locus		gami	Rainy	Bad	White	stiquia	wana	Goulais	Stur	Pic	inee	Wolf	saugi	wasaga	Spanish	Detroit	Clair	Niagara	Prairies	Law
	е	(0.00)	(0.00)	(0.02)	(0.00)	(0.05)	(0.30)	(0.45)	(0.35)	(0.09)	(0.48)	(0.49)	(0.48)	(0.40)	(0.53)	(0.36)	(0.42)	(0.51)	(0.48)	(0.50)
AfuG 122	0	0.21		0.20	0.08	0.38	0.83	0.25	0.28	0.38	0.48	0.40	0.31	0.57	0.00	0.28	0.11	0.20	0.62	0.51
	е	(0.62)	(0.76)	(0.64)	(0.70)	(0.73)	(0.73)	(0.69)	(0.58)	(0.74)	(0.61)	(0.66)	(0.75)	(0.71)	(0.00)	(0.73)	(0.62)	(0.72)	(0.73)	(0.80)
Spl 120	0	0.75	0.56	0.76	0.57	0.65	1.00	0.74	0.67	0.48	0.72	0.67	0.57	0.86	0.60	0.73	0.67	0.79	0.64	0.69
	е	(0.75)	(0.70)	(0.76)	(0.69)	(0.65)	(0.55)	(0.66)	(0.73)	(0.62)	(0.70)	(0.69)	(0.62)	(0.81)	(0.60)	(0.65)	(0.63)	(0.79)	(0.71)	(0.74)
Average Observed Heterozygosity		0.48	0.46	0.52	0.47	0.52	0.59	0.58	0.54	0.47	0.51	0.50	0.50	0.58	0.64	0.50	0.54	0.60	0.57	0.56

Table 4. Population differentiation. Pairwise F_{ST} values are below the diagonal and p-values are above the diagonal. P-values were calculated based on 3420 permutations. F_{ST} values in bold and shaded yellow, and p-values in bold are **NOT** significant, indicating those populations cannot be genetically differentiated (p>0.0015; significance cut-off determined after sequential Bonferroni correction).

	Matta-				Kamini-	Batcha-		Black		Menom-		Missis-	Nottawa	-		St.		Des	St.
	gami	Rainy	Bad	White	stiquia	wana	Goulais	Sturgeon	Pic	inee	Wolf	saugi	saga	Spanish	Detroit	Clair	Niagara	Prairies	Lawrence
Mattagami		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.002	0.00	0.00	0.00	0.00	0.00
Rainy	0.10		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.004	0.00	0.00	0.00	0.00	0.00
Bad	0.15	0.17		0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
White	0.18	0.19	0.01		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.004	0.00	0.00	0.00	0.00	0.00
Kaministiquia	0.14	0.15	0.11	0.13		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Batchawana	0.18	0.20	0.12	0.12	0.11		0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00
Goulais	0.16	0.19	0.09	0.09	0.08	0.03		0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.004	0.00
Black Sturgeon	0.15	0.13	0.12	0.13	0.11	0.07	0.08		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pic	0.15	0.14	0.11	0.12	0.07	0.05	0.05	0.03		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Menominee	0.19	0.20	0.14	0.15	0.12	0.07	0.07	0.07	0.05		0.00	0.00	0.003	0.03	0.00	0.00	0.00	0.003	0.00
Wolf	0.17	0.19	0.12	0.13	0.11	0.07	0.04	0.09	0.07	0.04		0.00	0.00	0.08	0.00	0.00	0.00	0.003	0.00
Mississaugi	0.16	0.17	0.13	0.13	0.10	0.03	0.03	0.07	0.04	0.04	0.03		0.02	0.65	0.00	0.00	0.00	0.00	0.00
Nottawasaga	0.18	0.19	0.09	0.11	0.09	0.06	0.04	0.06	0.03	0.03	0.03	0.01		0.05	0.24	0.20	0.02	0.03	0.00
Spanish	0.20	0.25	0.17	0.16	0.14	0.05	0.01	0.10	0.08	0.07	0.08	0.01	0.06		0.11	0.12	0.21	0.68	0.05
Detroit	0.15	0.17	0.11	0.12	0.08	0.05	0.03	0.09	0.04	0.05	0.05	0.02	0.00	0.02		0.21	0.04	0.00	0.00
St. Clair	0.16	0.16	0.12	0.12	0.09	0.04	0.04	0.06	0.04	0.04	0.05	0.02	0.00	0.01	0.00		0.03	0.00	0.00
Niagara	0.15	0.15	0.10	0.10	0.08	0.06	0.03	0.08	0.06	0.06	0.04	0.02	0.02	0.02	0.01	0.01		0.01	0.00
Des Prairies	0.12	0.15	0.09	0.09	0.09	0.04	0.02	0.07	0.04	0.03	0.02	0.01	0.01	0.02	0.03	0.03	0.01		0.21
St. Lawrence	0.16	0.17	0.13	0.14	0.11	0.06	0.06	0.09	0.06	0.04	0.03	0.03	0.02	0.04	0.04	0.03	0.03	0.01	

Figure 1. UPGMA tree showing genetically similar groups, based on Nei's unbiased genetic distance (1978). The top scale represents genetic distance values. Numbers correspond to bootstrap values, or the percentage of trees (out of 1000) where the corresponding split in the tree is confirmed. Only bootstrap values greater than 50% are displayed. Colors represent different lake basins: Lake Superior, Lake Michigan, Lake Huron, Lake Erie, Lake Ontario/St. Lawrence, and Hudson Bay.

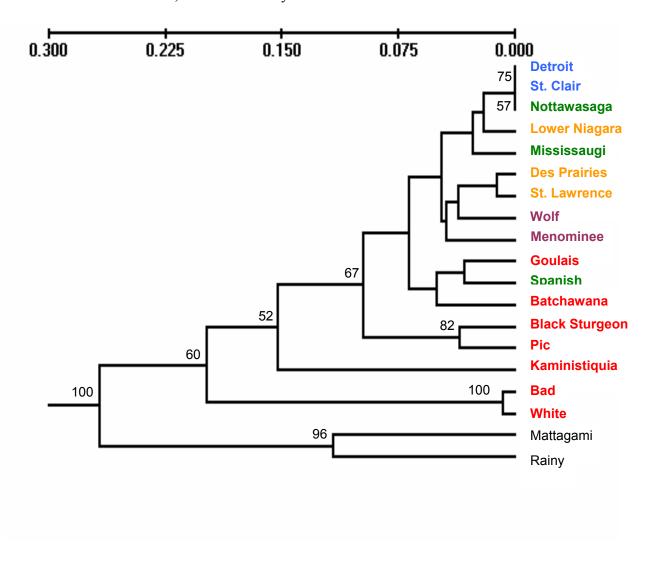


Figure 2. Neighbor-joining tree showing genetically similar groups, based on Cavalli-Sforza & Edwards' (1967) chord distance. This tree results from an approach similar to the one used to generate Figure 1; however, there are differences between the genetic distance measures used and assumptions behind the tree construction method. Numbers correspond to bootstrap values, or the percentage of trees (out of 1000) where the corresponding branch on the tree is confirmed. Only bootstrap values greater than 50% are displayed. Colors represent different lake basins: Lake Superior, Lake Michigan, Lake Huron, Lake Erie, Lake Ontario/St. Lawrence, and Hudson Bay.

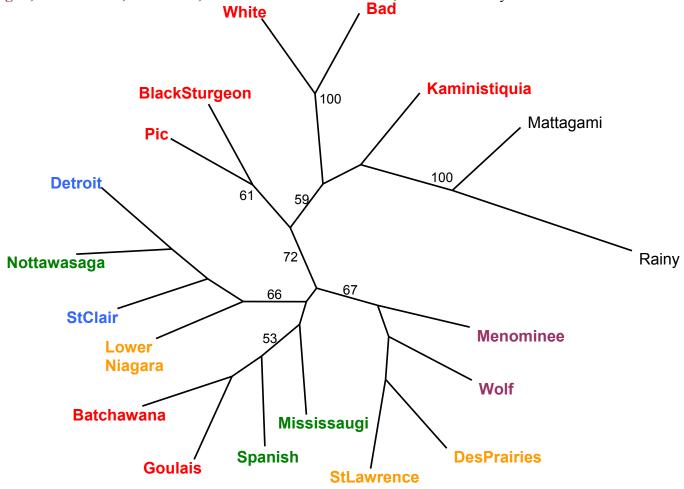


Figure 3. Factorial correspondence analysis showing genetic variation summarized in three components that account for approximately 56% of the genetic variation. Group means are displayed and the most distinguishable populations labeled. Note the distinctness of the Bad and White Rivers from the remainder of the populations.

